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Notes on the genus *Herberta*, with a revision of the species known from Europe, Canada and the United States*

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(WITH PLATE 8 AND 29 TEXT FIGURES)

INTRODUCTION

The genus *Herberta* (or *Herbertus*, as it was originally spelled) was published by S. F. Gray in 1821.† It was named in honor of George Herbert, one of the patrons of Micheli, and was based on a single species, the *Jungermannia adunca* of Dickson. In common with Gray's other genera, *Herberta* was ignored by botanical writers until Carruthers called attention to it in 1865.‡ Although it has since been accepted more or less widely in both Europe and North America, a strong tendency has recently arisen to repudiate it. This is largely due to Gray's unfortunate practice of giving his generic names a masculine termination, even when he derived them from the names of persons. As Dumortier expresses it, they are the names of men and not of plants. Since, however, a change from a masculine to a feminine termination might readily be construed as the correction of an error in orthography, this objection seems hardly sufficient to justify the setting aside of Gray's genera altogether. From a scientific standpoint the claims of *Herberta* are fully as good as those of many other genera which are accepted without question, and the writer is therefore disposed to recognize it, at least for the present.

A year after the appearance of *Herberta*, Dumortier§ published his genus *Schisma*, including under it not only *J. adunca* but also *J. juniperina* Sw. and *J. concinnata* Lightf. Nine years later he added another species, *S. stramineum* Dumort.,|| but excluded *J. concinnata*, making it the type of his new genus *Acolea*. At

* Contribution from the Osborn Botanical Laboratory.

† Nat. Arr. British Pl. 1: 705. 1821.

‡ Jour. Bot. 3: 300. 1865.

§ Comm. Bot. 114. 1822.

|| Syll. Jung. 76. 1831.

that time he was undoubtedly ignorant of Gray's writings. Many years afterwards, however, in his last published work on the Hepaticae,* he quotes Gray's generic names as synonyms, refusing to recognize them as valid on account of their masculine form. In the present instance he naturally maintains his genus *Schisma*. Gray's genera were likewise unknown to Nees von Esenbeck. In the first volume of his *Naturgeschichte der europäischen Lebermoose*, published in 1833, he accepted *Schisma* as valid (p. 107). In the third volume, published in 1838, he suggested that it might be considered a section of his genus *Mastigophora* (p. 573), although he continued to employ *Schisma* as a generic name. The inclusion of *Schisma* under *Mastigophora* would have been quite unwarranted on the basis of priority. The latter genus was not published until 1833, and its characters were completely revised in 1835. *Schisma* therefore antedates it by more than a decade. As originally defined *Mastigophora* was essentially the equivalent of the genus *Lepidozia* Dumort., although no species were definitely assigned to it; in its revised form it was made to include such species as *Jungermannia diclados* Brid. and *J. Woodsii* Hook. At the present time it is accepted by most writers in its revised form.

Nees von Esenbeck's provisional reduction was adopted definitely by the authors of the *Synopsis Hepaticarum* (1845), who went even farther than he and included both *Schisma* and *Mastigophora* under the genus *Sendtnera* of Endlicher,† a genus which had been proposed a few years earlier for the single species *Jungermannia Woodsii*. On account of the high position which the *Synopsis* holds in the literature of the Hepaticae the name *Sendtnera* was acknowledged for many years as the correct name for the combined genus. Now, however, both *Schisma* and *Mastigophora* are universally regarded as distinct, and the name *Schisma* is employed by those who refuse to sanction the use of the name *Herberta*.

Of the eighteen species of *Sendtnera* given in the *Synopsis* only six would now be included in the genus *Herberta*. In Stephani's recent monograph of the genus (under the name *Schisma*), pub-

* Bull. Soc. Bot. Belgique 13: 123. 1874.

† Gen. Plant. 1342. 1840.

lished in 1909,* seventy-one species are recognized. According to the information at hand four species have since been described, making seventy-five in all. This marked increase is due partly to the more extensive material at the disposal of recent writers and partly to their narrower interpretation of species. Of the seventy-one species admitted by Stephani nearly all have a very limited geographical range and no fewer than forty-seven are described as new. Taking into account the species of his monograph and those since published, two are restricted to Europe, thirteen to Africa (including the Azores), sixteen to Asia (including the Philippines), seven to various islands of the Pacific, ten to tropical North America, and twenty-six to South America; Stephani gives one species a wider range, including Samoa, Tahiti, Hawaii, Japan, and Himalaya. It is interesting to note that he accredits no species to North America north of Mexico, although *H. adunca*, a species which he restricts to Europe, has been repeatedly reported by American writers, not only from Alaska and British Columbia but also from the eastern United States.

The species of *Herberta* grow on rocks, on trees, and on the ground and sometimes form extensive mats or tufts. In the tropics they seem to be confined to higher altitudes, but the few species which occur in temperate and frigid regions sometimes descend to the level of the sea, this being true in both hemispheres. The plants are usually marked by a yellowish or brownish color, due to a pigmentation of the cell walls. In rare cases a reddish or purplish tinge is present, and in sheltered stations the pigmentation may be so slight that the plants appear green.

NOTES ON THE MORPHOLOGY OF THE GENUS

In its morphological features *Herberta* is one of the most clearly defined and natural genera of the Hepaticae. The gametophyte consists of a prostrate rhizome which gives rise to numerous secondary stems. These sometimes remain simple, even when they become comparatively long, and sometimes branch sparingly. The subequally bifid leaves are slightly incubous while the underleaves are strictly transverse, and yet, since the underleaves are nearly or quite as large as the leaves and similar to them in most

* Spec. Hepat. 4: 1-30. 1909.

other respects, the shoots appear almost radial in structure. The inflorescence is invariably dioicous. The androecium is at first terminal on a secondary stem or one of its branches but soon proliferates, and the male shoot eventually shows a series of short intercalary androecia separated by equally short sections bearing normal leaves. The archegonia are likewise terminal on secondary stems. When fertilization takes place the growth of the female stem is usually brought to an end; when fertilization does not take place one or more subfloral innovations may be produced. The involucre is composed of crowded bracts and bracteoles, which are essentially alike and not very different from the leaves, while the perianth is deeply lacinate at the mouth and free or nearly so from the bracts. The calyptra and the sporophyte conform to the usual jungermanniaceous type.

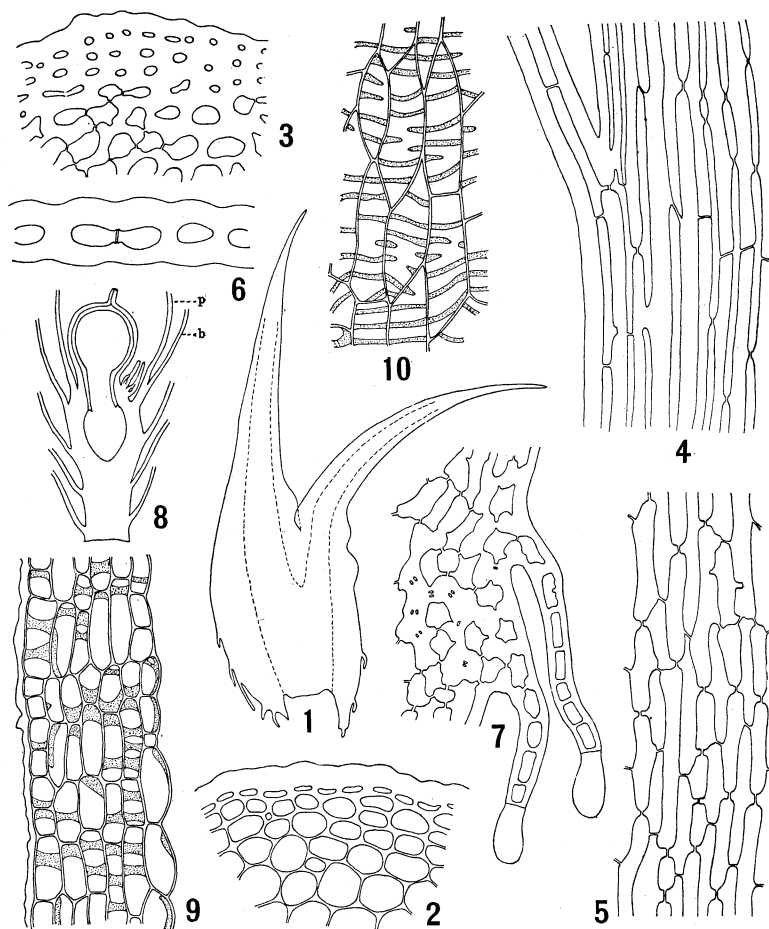
The rhizome of *Herberta* was apparently overlooked by the older writers. Spruce,* however, calls attention to it and to the fact that it may bear rhizoids, while Stephani mentions its small diameter and copious branching. It tends, in fact, to be considerably more slender than the secondary stems, although both vary in size. In *H. juniperina*, for example, an average rhizome measures only 0.35×0.25 mm. in cross section, while a stem measures 0.5×0.35 . The features of the rhizome are not easily made out in material where the secondary stems are well developed. The leaves are more or less disintegrated with age and it is difficult to demonstrate the relationship between the branches and the leaves. In most cases the leaves and underleaves are minute and widely separated. The leaves are practically transverse in their insertion and it would be difficult to distinguish them from the underleaves, if the rhizome did not show a slight dorsiventral flattening, the underleaves being of course situated on one of the flattened sides. Both leaves and underleaves are distinctly bifid. The rhizoids grow out normally from the basal cells of the underleaves, although they often occur on the leaves as well, but the rhizome itself is usually free from them. The branches are all intercalary and many of them spring from the axils of the underleaves. This position, however, is not constant; occasional branches tend to be lateral and do not show a definite relationship

* Trans. Bot. Soc. Edinburgh 15: 340. 1885.

to either leaves or underleaves. It is of course possible that their aberrant position is due to secondary displacements caused by inequalities of growth, but this could not be definitely determined from the material studied. The secondary stems are sometimes direct extensions of the creeping rhizomes, but it is usually possible to demonstrate their origin as branches. Even under these circumstances they usually bear small leaves at the base and only gradually give rise to the normal leaves. Sometimes the change is more abrupt, and all gradations may be present between the small-leaved prostrate rhizomes and the typical secondary stems with large leaves.

The secondary stems differ greatly in length in different species and even in the same species under varying conditions. In some of the robust tropical species a length of 25 cm. may be attained. The stems are usually ascending but are often pendulous and sometimes form conspicuous festoons hanging from the branches of trees. The branches are always intercalary, just as in the case of the rhizomes. The normal vegetative branches take their origin in the axils of underleaves and are rarely subdivided. In most cases they spread widely and show a flagelliform appearance, their leaves being distinctly smaller than those of the stem. When the growing point of a stem is injured, however, a ventral branch sometimes changes its direction of growth and assumes that of the stem, its leaves at the same time increasing in size. The same thing is true of the subfloral innovations, which may be either ventral or lateral in position. The growth of the stem is here brought to an end by the development of the archegonia. Rhizoids are often absent altogether from the secondary stems. When they occur they are usually restricted to the underleaves and leaves of the ventral branches, although the normal leaves and underleaves have the power of developing them.

The leaves (TEXT FIGS. 1, 14, 15, 21-25) and underleaves of the secondary stems present a great deal of uniformity throughout the genus. They are more or less deeply bifid with a narrow sinus and sharp divisions. In rare cases a leaf may be trifid instead of bifid, a peculiarity to which certain species seem to be more subject than others. The divisions are sometimes distinctly grooved but show little tendency to be complicate, both lying approximately in

FIGS. 1-10. *HERBERTA JUNIPERINA* (Sw.) Trevis.

1. Leaf, $\times 17$. 2. Transverse section of a young stem, $\times 225$. 3. Transverse section of a mature stem, $\times 225$. 4. Longitudinal section of a mature stem, including the base of a leaf, $\times 225$. 5. Cells from the basal vitta of a leaf, $\times 225$. 6. Cells from the basal vitta of a leaf in transverse section, $\times 300$. 7. Cells from the dorsal base of a leaf, showing cilia with slime papillae, $\times 225$. 8. Longitudinal section of a young sporophyte and surrounding parts, $\times 17$; *b*, innermost perichaetial bract; *p*, perianth. 9. Transverse section of the wall of a mature capsule, $\times 225$. 10. Cells from the innermost layer of the wall of a mature capsule, $\times 225$. FIGS. 1, 5-7 were drawn from specimens collected by the writer on Blue Mountain Peak, Jamaica, 242; FIGS. 2-4, 6, from specimens collected by L. M. Underwood along the trail from Cinchona to Morce's Gap, Jamaica, 280; the remaining figures, from specimens collected by W. Harris on the lower slopes of Sir John Peak, Jamaica, 11133.

the same plane. At the base on each side a series of slime papillae or their vestiges can be demonstrated. These are sometimes sessile (TEXT FIG. 17) and sometimes borne on the tips of more or less evident teeth or cilia (TEXT FIG. 7; PLATE 8, FIG. 5). Occasionally slime papillae with their teeth are developed on the surfaces of the leaves and underleaves, as well as on their margins. The teeth vary from short stalks a cell or two long to broad and subdivided lobe-like structures. Except for the basal teeth associated with the slime papillae the margins are usually quite entire. In a few species, however, distinct teeth are present higher up, even beyond the region of the sinus, and these teeth show no evidences of slime papillae. Even when teeth of this character are present the upper parts of the divisions lack them completely. A vague serrulation, caused by projecting cells, may sometimes be discernible but seems to be a very exceptional feature.

Aside from the difference in insertion there are certain other slight differences between the leaves and underleaves. The leaves are usually curved backward and appear unsymmetrical when dissected from the stems and spread out flat. The curvature affects the ventral division more strongly than the dorsal division (PLATE 8, FIGS. 1-3); the latter in fact may be straight or nearly so while the ventral division is strongly curved (TEXT FIG. 1). In some species the curvature is much less pronounced than in others and may not be evident at all in explanate leaves (TEXT FIGS. 22-25); the lack of symmetry, however, still expresses itself in a difference of direction of the divisions and in a greater development of the basal portion on the dorsal side. The underleaves bend backward in a squarrose fashion and appear symmetrical when spread out, their straight divisions diverging equally and the basal portion being equally developed on the two sides. The leaves and underleaves are usually more or less imbricated. The divisions of the curved leaves and squarrose underleaves are thus crowded together along the ventral portion of the shoot, the plant acquiring a distinctly moss-like appearance.

The cells and especially the cell-walls yield some of the most distinctive characters of the genus. Most of the walls are strongly thickened and this applies even to the rhizoids when they become

old. According to Goebel* excessive thickening of the cell walls in the bryophytes, which occurs especially in xerophilous species, is significant on account of the great power of imbibition which these walls possess. They readily absorb and retain water, and the rapidity with which most species of *Herberta* regain their normal appearance and consistency, when a dry tuft is deluged with water, is a striking phenomenon. In the cauline portions of the plant the cells are all elongated, although they never assume a truly prosenchymatous character. The outer or cortical region is distinguished from the inner or axial region by its deeper color and more strongly thickened walls. In the secondary stems the thickening at first takes place in the outermost layer of cells, the process continuing until the cell cavities become reduced to narrow canals (TEXT FIG. 2). The thickening is largely restricted to the outer or superficial walls and the layer presents the appearance of an epidermis with well-developed cuticle. In some cases the entire cortex consists of this outermost layer, the walls of the remaining cells showing only a slight degree of thickening (TEXT FIG. 26). This, however, is very unusual. In the majority of cases two or more additional layers take part in the formation of the cortical region; their walls become as markedly thickened as those of the outermost layer, the only difference being that the thickening is deposited uniformly on all the walls (TEXT FIG. 3). Even in the central region the thickening of the walls is sometimes very pronounced, though never so much so as in the cortical region. Since, moreover, the central cells are larger than the cortical cells, their cavities remain distinctly wider. The cells of the stem are everywhere connected by pits, which show clearly in both transverse and longitudinal walls (TEXT FIGS. 3, 4). They are just as evident in the superficial layer as elsewhere, the cells of this layer being connected with one another both longitudinally and tangentially, as well as with the cells of the layer next within. There is nothing, in fact, to indicate any essential difference in function between the superficial layer and the other cortical layers. In spite of the fact that the outer walls simulate a cuticle so strongly, they have the same powers of imbibition as the other walls and simply form part of the imbibing system of the stem. In the rhizomes the

* See Organographie der Pflanzen, 2d ed. 553. 1915.

same distinction between cortical and central regions is apparent. There is perhaps a tendency for the cortical region to be thinner and for the cell-walls of the central region to be less thickened than in the secondary stems, but there are no essential differences between the two.

The leaf-cells in their more important features have long been familiar to students of the Hepaticae. Although forming a single layer as in most of the Jungermanniaceae the cells show a differentiation into elongated cells and more or less isodiametric cells (see, for example, PLATE 8, FIG. 4). The elongated cells form a median band extending from the line of insertion into the basal portion of the leaf. Somewhere below the sinus the band, or "vitta," as Stephani terms it, forks, one branch passing into each division. Here they may extend to the extreme apices or stop at a variable distance below them. The isodiametric cells form the rest of the leaf and are divided into three patches by the vitta and its branches, the two lateral patches extending from the base into the divisions on their outer sides and the median patch from the forking of the vitta into the divisions on their inner sides. Apparently the first allusion to the vitta is found in the original description of *H. dicrana* (Tayl.) Trevis.* In a critical note, quoted from Taylor, a "nerve" is spoken of which runs out into the divisions. Gottsche afterward described the vitta in other species, and Stephani lays especial emphasis on it in his recent monograph. In his opinion the vitta yields some of the best differential characters in distinguishing species. He considers the basal portion (below the forking) to be constant in size for a given species, and he finds an equal constancy in the length of the branches. Unfortunately it is not always easy to determine the exact lateral boundaries of the vitta or the points where the branches terminate in the divisions of the leaves. Although the median cells of the basal portion are markedly different from the cells near the margin of the leaf, there is sometimes a gradual transition between the vitta and the marginal portion, and a similar transition may exist between the cells of the vitta and the marginal and apical cells of the divisions. Two observers, in consequence, might obtain different results in measuring the same

* Syn. Hep. 239. 1845.

leaf. A case in point is found in *H. adunca*. According to Stephani the branches of the vitta come to an end below the apices of the divisions; according to K. Müller they extend to the apices. At the same time the value of the vitta from the standpoint of taxonomy must not be overlooked, and Stephani deserves credit for utilizing it.

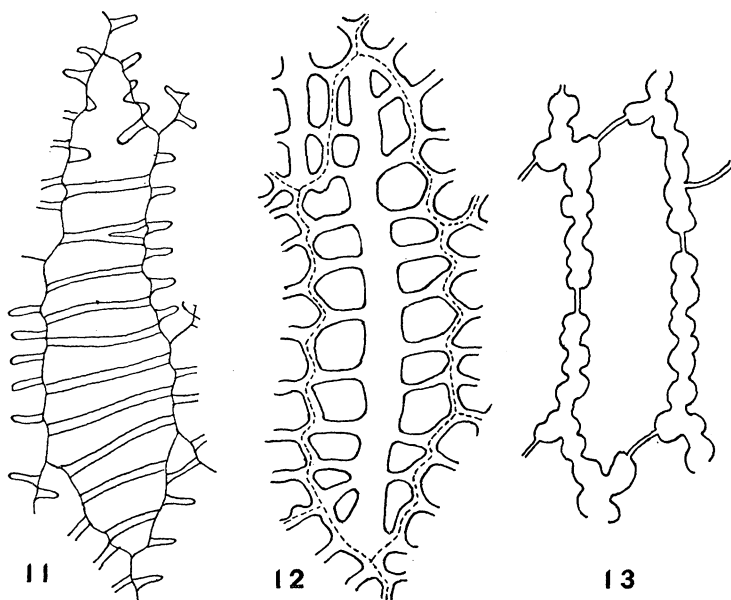
The cells of the vitta present a number of interesting peculiarities, not only in their structure at maturity but also in their development, especially in the way in which the thickenings of the wall are deposited. Gottsche, in his account of *H. juniperina*,* noted some of these peculiarities many years ago, but subsequent allusions to them have been very scanty. According to Gottsche each basal cell of the leaf, after treatment with caustic potash and iodide of zinc, reveals a spiral of eight to fifteen turns representing a thickening of the secondary layer of the wall. In a later account† of the same species he gives the number of turns as fifteen to twenty-two.

By treating young leaves with potash it is easy to demonstrate the presence of the bands of thickening described by Gottsche, not only in the basal portion of the leaf but elsewhere, and they clearly represent a stage in the development of the cell wall (TEXT FIG. 11). The writer has found it impossible, however, to show that the bands form a continuous spiral. They seem to be rather in the form of separate rings or partial rings, an occasional ring being branched. When the rings are incomplete the gaps occur on the free walls of the cell and never on the vertical walls, which separate the cell from its neighbors. Even under these circumstances, however, the bands of thickening extend partially across the free walls and leave only the median portion thin throughout. The bands of one cell do not lie opposite the bands of adjoining cells but tend to alternate with them. The vertical walls show a zigzag appearance where they meet the free walls, each angle of the zigzag marking the position of one of the bands. In the irregular cells between the vitta and the margin the bands are more irregular than in the cells of the vitta and rarely if ever form complete rings. In other respects they are essentially the same.

* Rabenhorst, Hep. Eur. 210, accompanying text.

† Mex. Leverm. 138. 1863.

The bands of thickening just described soon become united by median bands laid down on the free walls (TEXT FIG. 12). These leave a series of thin places on each side, which show at first angular outlines. Almost simultaneously the bands on the vertical walls increase in thickness and become connected by deposits laid down between them, the result being that these walls acquire a



FIGS. 11-13. *HERBERTA JUNIPERINA* (Sw.) Trevis.

11. Very young cell from the basal vitta of a leaf, surface view, $\times 1,000$. 12. Somewhat older cell from same vitta, surface view, $\times 1,000$. 13. Still older cell from same vitta, optical section, $\times 600$. The figures were all drawn from specimens collected by L. M. Underwood along the trail from Cinchona to Morce's Gap, Jamaica, 280.

continuous layer of thickening except for an occasional pit. At first the original bands are thickened more conspicuously than the intermediate regions and the vertical walls appear distinctly scalloped when examined in optical section (TEXT FIG. 13). But the conditions just described are temporary. The thin places in the free walls are gradually filled up by deposits of thickening, becoming rounded as they diminish in size, and the depressions between the scallops along the vertical walls become obliterated

in much the same way. The entire cell-cavity is eventually lined by a uniformly thick layer of deposit, the only thin places left being the pits in the vertical walls (TEXT FIGS 5, 6). Even some of the pits may be obliterated with age. When this takes place the deposit either fills the pit-chamber altogether or bridges it across, leaving a minute vestige of the chamber next to the closing membrane (TEXT FIG. 7). When the cells are mature it is sometimes possible to detect evidences of the original bands of thickening and of the scallops along the vertical walls, but the free walls present an absolutely uniform appearance. Although the thickenings look very much as if they were formed by the coalescence of trigones and intermediate thickenings, it is clear from their method of development that they are not directly comparable with the trigones and intermediate thickenings of other Hepaticae.

Although the description just drawn from *H. juniperina* probably applies in its essential features to the entire genus, the details are not always as clear in some of the other species. In *H. adunca*, for example, it is difficult to demonstrate bands of thickening except in the basal portion of the vitta, and it is doubtful if they ever form complete rings. The scalloped appearance of the vertical walls is likewise much less evident. Possibly the more indefinite conditions found are associated with the fact that the thickening of the walls in *H. adunca* is usually much less marked than in *H. juniperina*.

The leaf surface in *Herberta*, the so-called cuticle of authors, is striolate or verruculose. The roughness is sometimes very apparent and sometimes made out with difficulty. Whether differences in the degree of roughness yield constant differential characters in separating species is perhaps doubtful, although such differences seem very striking when certain species are compared.

The androecia in *Herberta* are relatively short and usually include from four to eight pairs of bracts, those at the upper and lower ends being somewhat transitional in character. The male plants tend to produce smaller leaves than female plants or vigorous sterile plants, and although the bracts are considerably larger than the leaves borne between the successive androecia, they scarcely equal in size the normal leaves on female individuals. Several years ago Schiffner made the remarkable discovery that

antheridia occur not only in the axils of the bracts but also in the axils of the bracteoles.* In order to determine whether this phenomenon was widespread among the Ptilidioideae, to which group *Herberta* is usually assigned, he examined species of several other genera. The closely related *Mastigophora*, however, was the only one in which he was able to observe antheridial bracteolès. In the case of *Herberta* the bracteoles differ from the bracts in about the same way that the ordinary underleaves differ from the leaves. Both bracts (TEXT FIG. 20; PLATE 8, FIGS. 8, 9) and bracteoles are more or less imbricated and have a broad inflated pocket at the base enclosing a cluster of two or more antheridia. The pocket does not involve the entire width of the basal region but leaves a narrow flattish or revolute strip on each side. In the inflated portion the cells are broader and much paler than ordinary cells, and the thickenings of the walls are more irregular in outline and less strongly developed. The divisions, sinus, and margins are much the same as on ordinary leaves.

The perichaetial bracts (PLATE 8, FIGS. 10, 11) and bracteoles are essentially alike. They occur in three or four closely crowded series and increase somewhat in size toward the perianth, only the apical portion of which projects beyond them. Those of the innermost series, when viewed from the outer surface, show two rounded ridges in the basal portion, separated by a narrow median groove. A marginal band on each side is flat or slightly concave. The divisions are much the same as on ordinary leaves but the margins are much more toothed, the teeth being irregular and extending higher up, sometimes almost to the apices of the divisions. Occasionally minute and irregular paraphyllia (PLATE 8, FIG. 12) with marginal papillae are found among the bracts. According to Spruce the bracts closely embrace the perianth but are free from it throughout their entire length; according to Stephani they are coalescent with the perianth up to a considerable height. A longitudinal section through a young sporophyte and surrounding parts (TEXT FIG. 8) shows that Spruce was essentially correct. Any coalescence which may be present is so slight as to be practically negligible. Between the innermost bracts and bracteole and the leaves below the involucre there is a gradual transition.

* Untersuchungen über Amphigastrial-Antheridien und über den Bau der Andröcien der Ptilidioideen. *Hedwigia* 50: 146-162. f. 1-39 1910.

The perianth of *Herberta*, when well developed, clearly supports the theory that three floral leaves take part in the formation of this organ (PLATE 8, FIG. 13). It is split for nearly half its length into six slender laciniae, essentially like divisions of leaves, every alternate split being a little deeper than the others. These deeper splits mark the boundaries of the three coalescent leaves. In the undivided portion of the perianth a cross section shows that six rounded ridges are present, separated by six rounded grooves (PLATE 8, FIG. 14). Three alternate grooves are deeper than the others and correspond with the three deeper splits at the mouth of the perianth. The innermost bracts and bracteoles, each with its two dorsal ridges separated by a groove, are closely appressed to the ridges and grooves of the perianth. The laciniae of the perianth bear numerous slime-papillae and often teeth. The slime papillae occur not only along the margins of the laciniae toward the base but also on the inner surface of the perianth. Here they sometimes form short rows and sometimes show no regular arrangement. The surface papillae are occasionally borne on the tips of short teeth or along the margins of narrow and irregular ridges. In some cases the perianth is not developed normally. More than six laciniae, for example, may be present at the mouth, or one of the splits may extend to the very base; sometimes both of these abnormalities may be seen in a single perianth. An increase in the number of laciniae is not surprising, since ordinary vegetative leaves with three divisions sometimes occur, and the deep split might plausibly be interpreted as a place where coalescence had failed to take place.

The wall of the capsule is described in its essential features by Spruce. It is composed of from five to seven layers of cells (TEXT FIG. 9) and shows a thickness of 70–100 μ . This is considerably more than in most of the leafy Hepaticae studied by Andreas.* In *Plagiochila asplenoides* (L.) Dumort., for example, where the wall is composed of seven or eight layers, the thickness is only 55 μ , while in *Chiloscyphus polyanthus* (L.) Corda, where the wall is composed of five layers, the thickness is only 25 μ . It is less, however, in *Herberta* than in *Pleurozia purpurea* (Lightf.)

* Ueber den Bau der Wand und die Oeffnungsweise des Lebermoossporogons. Flora 86: 161–213. pl. 12 + f. 1–25. 1899.

Lindb.; in this species, according to Andreas, the wall is composed of seven or eight layers and has a thickness of $130\ \mu$. In all these forms he describes local thickenings in the cells of all the layers. In the innermost layers the thickenings are in the form of half rings extending across the inner tangential wall (see TEXT FIG. 10) In the other layers they are in the form of bands on the radial walls. Even here, however, the bands sometimes extend to a greater or less extent along the tangential walls. According to Andreas the structure of the capsule wall in the leafy Hepaticae shows comparatively little variation, and the genus *Herberta* agrees on the whole with his account. It might be added that the valves are covered on the outside by a granular wax-like deposit, and that secondary splits sometimes occur in one or more of the four primary valves.

Many years ago Spruce* described the occurrence of rudimentary shoots on the leaves of *Herberta*. According to his account they arise singly or in pairs from the cells of the vitta in the basal portion of the leaves and never in the divisions. These shoots have not been observed by the writer and are probably developed under exceptional conditions. They represent the only type of vegetative reproduction known in the genus. As Spruce's figures clearly show, the shoots bear three ranks of small bifid leaves and show no signs of dorsiventrality. They resemble in many respects the adventive shoots borne on the leaves of certain species of *Plagiochila*, although they are much less abundantly produced.

REVISION OF THE SPECIES KNOWN FROM EUROPE, CANADA AND THE UNITED STATES

According to most recent writers on the Hepaticae the genus *Herberta* is represented in Europe by only two species. The first of these is *H. adunca* (Dicks.) S. F. Gray, the type of the genus; the second, *H. Sendtneri* (Nees), sometimes known as *H. straminea* (Dumort.) Trevis. The range of *H. adunca*, according to available records, is restricted to Norway, the Faroe Islands and the British Isles; the range of *H. Sendtneri* is even more circumscribed, being accredited only to the Austrian and Bavarian Alps.

* On the branch-bearing leaves of *Jungermannia juniperina*, Sw. Phytologist 2: 85, 86. 1844. [Illust.]

In thus restricting the range of the latter species, writers differ markedly from Dumortier.* He considered that his *Schisma stramineum*, under which he included *S. Sendtneri* Nees as a synonym, grew in Scotland, as well as in Austria and Germany. His species, in fact, was based on Scottish material. Apparently his only recent follower is Lett,† who admits both *H. adunca* and *H. straminea* as members of the Scottish flora.

Botanists have long recognized the fact, however, that *H. adunca* includes two well-marked forms. These were distinguished by Gottsche,‡ as long ago as 1862, under the names, α *Dicksoniana* and β *Hutchinsiae*. He applied the first name to the plant with shorter, erect-spreading leaves, having straight acuminate divisions, and the second to the plant with longer leaves, hooked when dry and squarrose when moist, having lanceolate, incurved divisions. He considered that α *Dicksoniana* was primarily a plant of Scotland while β *Hutchinsiae* was primarily a plant of Ireland, and yet he made no attempt to restrict the range of either form definitely. Carrington,§ in taking up the name β *Hutchinsiae*, implies that all the Irish specimens are referable to this form and states that the species grows at much lower altitudes in Ireland than in Scotland. He adds that both forms grow in Scotland, the form with ovate or ovate-lanceolate leaves being restricted to higher and exposed mountains. This form is clearly Gottsche's α *Dicksoniana*, although Carrington does not call it by this name. He includes under it Dumortier's *S. stramineum* as a synonym and calls attention to the fact that it approaches *H. Sendtneri*. Although subsequent British writers have paid little attention to Gottsche's names, Schiffner has recently revived them and applied them to specimens in his exsiccatae.||

From a careful study of European specimens referred to *H. adunca*, the writer has reached the conclusion that Gottsche's two so-called forms represent two distinct, but closely related, species. The form α *Dicksoniana*, as its name implies, represents the type of *Jungermannia adunca* Dicks. In the absence of Dickson's original

* Bull. Soc. Bot. Belgique 13: 125. 1874.

† Hepat. British Isl. 177. 1902.

‡ Rabenhorst, Hep. Eur. 210. 1862.

§ Trans. Bot. Soc. Edinburgh 7: 454. 1863.

|| Hep. Eur. Exsic. 403-407. 1912.

material, the statement is supported by Scottish specimens in the Taylor herbarium, received from Hooker, and by the fact that Dickson's plant was collected "in albus Scotieis." The type of Dumortier's *Schisma stramineum* was likewise collected "in albus Scotiae" and, in the complete absence of all of Dumortier's types, his species may be regarded as a simple synonym of *H. adunca*. The second form, β *Hutchinsiae*, is described below as a new species under the name *H. Hutchinsiae* (Gottsche). In certain respects the true *H. adunca*, as thus restricted, resembles *H. Sendtneri* more strongly than it does *H. Hutchinsiae*. This would account for the fact that Dumortier failed to distinguish between his *Schisma stramineum* and *H. Sendtneri*. The latter species, however, is clearly distinct, and there is no evidence that its range extends beyond the mountains of Austria and Germany.

With regard to the North American specimens which have been referred to *H. adunca*, there has likewise been confusion. There are apparently two species represented, but neither agrees with typical *H. adunca*. The plant from the eastern United States seems to be new and is described below under the name *H. tenuis*; the plant from the Pacific Coast, on the contrary, seems to be referable to *H. Hutchinsiae*. The Alaskan material of this species is unusually satisfactory because it shows androecia, perianths, and sporophytes, all of which are exceedingly rare in European material. The four species considered in the present paper may be distinguished as follows, only vegetative characters being used:

Leaves mostly 1.2–2 mm. long and 0.45–0.9 mm. wide.

Leaves bifid about one half; divisions broad, slightly or not at all curved, acute to acuminate; vitta not distinct, the cells in the divisions mostly 20–40 μ long.

Basal portion of leaves normally entire.

1. *H. adunca*.

Basal portion of leaves sparingly and coarsely toothed.

2. *H. Sendtneri*.

Leaves bifid two thirds to four fifths; divisions narrow, strongly curved, long-acuminate; vitta distinct, the cells in the divisions often 50–70 μ long; basal portion of leaves entire or nearly so.

3. *H. Hutchinsiae*.

Leaves mostly 0.9–1 mm. long and 0.3–0.35 mm. wide, bifid two thirds to three fourths; divisions narrow, slightly or not at all curved, long-acuminate; vitta distinct, the cells in the divisions often 50–70 μ long; basal portion entire or sparingly and coarsely toothed.

4. *H. tenuis*.

1. HERBERTA ADUNCA (Dicks.) S. F. Gray

Jungermannia adunca Dicks. Plant. Crypt. Brit. 3: 12. *pl.* 8, *f.* 8. 1793.

Jungermannia juniperina β Hook. Brit. Jung. *pl.* 4. 1812 (in part).

Herberta adunca S. F. Gray, Nat. Arr. Brit. Pl. 1: 705. 1821.

Schisma aduncum Dumort. Comm. Bot. 114. 1822.

Jungermannia juniperina β *adunca* Lindenb. Nova Acta Acad. Leop.-Carol. 14 (suppl.): 35. 1829 (in part).

Schisma stramineum Dumort. Syll. Jung. 76. 1831; Bull. Soc. Bot. Belgique 13: 125. 1874 (in part).

Schisma juniperinum β Nees, Naturg. Europ. Leberm. 1: 108. 1833.

Sendtnera juniperina β Nees; G. L. & N. Syn. Hep. 239. 1845.

Sendtnera straminea Nees, *l.c.* 240. 1845.

Sendtnera adunca α *Dicksoniana* Gottsche; Rabenhorst, Hep. Eur. 210 (accompanying text). 1862.

Herberta straminea Trevis. Mem. R. Ist. Lomb. III. 4: 396. 1877 (in part).

Herberta adunca var. *straminea* Cooke, Handb. Brit. Hepat. 70. 1894.

Herberta adunca var. *alpina* Macvicar, Student's Handb. Brit. Hepat. 340. 1912.

Herberta adunca α *Dicksoniana* Schiffn. Lotos 60: 53. 1912.

Yellowish or brownish green, often tinged with red or purple, sometimes slightly glossy, growing in more or less extensive mats, or scattered among other bryophytes: secondary stems erect or ascending, sparingly and irregularly branched, rigid, mostly 5–10 cm. long but sometimes shorter, about 0.25 mm. (or fourteen cells) wide and 0.18 mm. (or ten cells) thick, the cells everywhere with strongly thickened walls: leaves imbricated, more or less secund, unsymmetrical, ovate, mostly 1.2–1.4 long and 0.45–0.6 mm. wide, bifid about one half, the divisions (in explanate leaves) slightly or not at all curved, acute to acuminate, mostly 0.6–0.7 mm. long and 0.27–0.35 mm. wide at base, margin normally entire; vitta usually indistinct even in the basal region, extending for a short distance into the division but coming to an end considerably below the apex, undivided portion usually 0.2–0.3 mm. long and wide; cells of vitta mostly $35\text{--}60 \times 22 \mu$ in the basal portion and $20\text{--}40 \times 20 \mu$ in the divisions, marginal cells in basal portion

about $22\ \mu$ in diameter, cells between margin and vitta about $24\ \mu$ in diameter; thickenings distinct, in the vertical walls mostly $8-10\ \mu$ wide; cuticle scarcely striolate: underleaves similar to the leaves but squarrose and symmetrical: male inflorescences borne in an interrupted series in the upper part of a stem; bracts mostly in five or six pairs, similar to the leaves except for the broad basal pocket extending nearly to the sinus, margin normally entire; bracteoles similar to the bracts; antheridia mostly two or three in each axil: female inflorescence not seen. [TEXT FIGS. 14-20.]

The following specimens have been examined:

NORWAY: Drivandefossen Waterfall, Lyster, Bergen Stift, August, 1900, *B. Kaalaas* (listed by Kaalaas in *Nyt. Mag. f. Naturv.* 40: 247. 1902; distributed as *H. adunca* α *Dicksoniana* in Schiffner's *Hep. Eur. Exsic.* 465); Söndfjord, Bergen Stift, July, 1903, *E. Jörgensen* (distributed as *H. adunca* α *Dicksoniana* by Schiffner, *l.c.* 464); Frafjord near Stavanger, July, 1899, *E. Jörgensen* (distributed as *H. adunca* α *Dicksoniana* by Schiffner, *l.c.* 463; specimens from same locality listed by Kaalaas, *l.c.* 33: 224. 1893).

FAROE ISLANDS: Syderö, Bordö and Vaagö, May and June, 1896, *C. Jensen* (these are among the specimens listed by Jensen in *Bot. Faer.* 1: 127. 1901).

SCOTLAND: Ben Lawers, 1803, *W. J. Hooker* (listed as *Jungermannia juniperina* β by Hooker in *Brit. Jung. pl.* 4. 1812); Craig Chailleach, *G. E. Hunt*; same locality, June, 1900, *S. M. Macvicar*; Camlochan, July, 1843, *W. Gardiner*; Stuichd-an-Lochain, July, 1842, *W. Gardiner*; near summit of Ben More, July, 1897, *H. N. Dixon* (var. *alpina* Macvicar); Glengyle, June, 1895, *Stirling & Kidston*; Ben Vorlich, July, 1901, *S. M. Macvicar* (listed in *Ann. Scottish Nat. Hist.* 1902: 114); Ben Udlaiddh, June, 1903, *S. M. Macvicar*.

WALES: Snowden Mountain, June, 1915, *A. H. Graves*.

In Ingham's Census Catalogue of British Hepatics, published in 1913, *H. adunca* is quoted from the following provinces: South Wales, North Wales, Lakes, East Highlands, West Highlands, North Highlands and North Isles. It is quoted also from eleven county divisions in Ireland. It is probable that some of these records, especially those from Ireland, are based on *H. Hutchinsiae*.

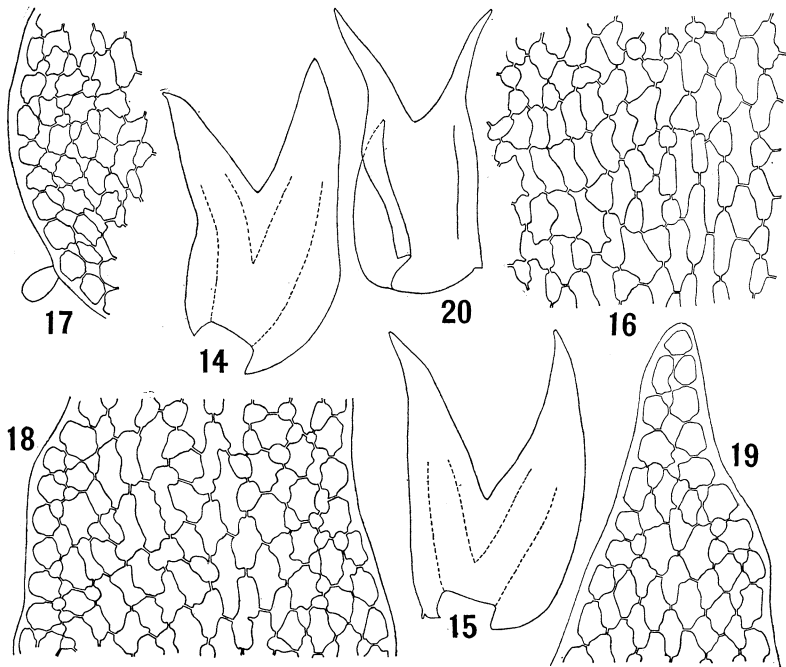
Most of the earlier writers not only failed to distinguish *H. Hutchinsiae* from *H. adunca* but considered the combined species a mere variety or form of the Jamaican *H. juniperina* (Sw.) Trevis. (*Jungermannia juniperina* Sw.). Hooker was apparently the first to advance this idea. In the text accompanying *pl. 4* of his British Jungermanniae he recognized *J. juniperina* as a member of the British flora and included *J. adunca* under the variety " β ," to which he did not even give a definite name. "After a most careful examination of Mr. Dickson's *J. adunca*, compared with others of *J. juniperina*, which I have received from Dr. Swartz," he adds in a critical note, "I am unable to find any characters which can induce me to keep them separate." He then calls attention to the larger size of the Jamaican plant and to the greater readiness with which it regains its original appearance when immersed in water but clearly regards these features of but little moment. Weber* protested against Hooker's treatment of *J. adunca* and maintained it as a valid species, in which he was followed by both S. F. Gray and Dumortier. The majority of contemporaneous writers, however, followed the example of Hooker, and the Synopsis Hepaticarum, in 1845, went so far as to cite Scottish specimens under *Sendtnera juniperina* β , without even mentioning *J. adunca* as a synonym. When Gottsche, nearly twenty years later, distinguished between his α *Dicksoniana* and β *Hutchinsiae*, he pointed out in addition the most marked differences between *H. adunca* and *H. juniperina*; and, since this time, both species have been almost universally recognized.

Among the characters of *H. adunca* which Gottsche emphasized was the lack of teeth on the leaves and underleaves. He pointed out the fact that young leaves sometimes showed five to eight primordial papillae at the base, these structures representing the rudiments of teeth, but of actual teeth he found no development. Although this description will apply to the vast majority of leaves, it will not apply to all. An occasional leaf will show one or perhaps two teeth in the basal region. Such a tooth usually consists of a single cell, serving as a stalk for a papilla, but it sometimes attains a length of several cells and becomes more lobe-like in appearance. The occurrence of these teeth, in view of their infrequency and

* Hist. Musc. Hepat. Prodr. 54. 1815.

irregularity, is doubtless more or less abnormal. The same thing may be said of the trifid leaves and of the blunt divisions which occasionally come to light, when a large series of leaves is examined.

Although Dickson's original figures show perianths and mature capsules, these organs seem to be very rarely produced.



FIGS. 14-20. *HERBERTA ADUNCA* (Dicks.) S. F. Gray

14, 15. Leaves, $\times 40$. 16. Cells from the basal portion of a leaf, showing the basal vitta on the right, $\times 225$. 17. Dorsal base of a leaf, $\times 225$. 18. Cells from the upper part of a dorsal leaf-division, $\times 225$. 19. Cells from the apex of the same division, $\times 225$. 20. Perigonial bract, $\times 40$. FIGS. 14, 16-19 were drawn from Norwegian specimens collected by E. Jørgensen and distributed in Schiffner's *Hep. Europ. Exsic. 464*; FIGS. 15, 20, from Norwegian specimens collected by B. Kaalaas and distributed in the same *exsiccatae 465*.

Hooker stated definitely that the only fruiting plants he had seen were Scotch specimens furnished by Dickson. Pearson* did not know fruiting plants at all; his description and figures of the bracts and perianths were drawn from Cuban specimens referred to *H. juniperina*, his idea being that the reproductive parts in this

* *Hep. British Isles 100, 101. pl. 36, f. 11, 12. 1900.*

species would not differ appreciably from those of *H. adunca*. Perianths were likewise unknown to Stephani, although he quotes from Kaalaas a brief description of bracts, perianths and capsule. Whether Kaalaas actually saw these structures in *H. adunca* is, however, doubtful. The description quoted by Stephani was taken (with certain arbitrary changes) from the account of the *genus* given by Kaalaas,* the account of the species merely stating that the reproductive organs were "ut in genere." According to Macvicar female plants are frequent, but perianths are unknown in the British Isles. He quotes Hooker's statement about Dickson's fruiting plants but suggests that there was probably some mistake on Dickson's part. If this idea could be substantiated there would be no evidence left that *H. adunca* had ever been found in fruit. It is to be hoped that further explorations may be rewarded by the discovery of the missing parts, although a persistent sterility would not be surprising in the present genus, where other well-marked species apparently produce neither archeogonia nor antheridia.

2. *Herberta Sendtneri* (Nees) comb. nov.

Schisma Sendtneri Nees, Naturg. europ. Leberm. 3: 575. 1838.

Jungermannia Sauteriana Hüben. & Genth, Deutschl. Leberm.

108. 1839 (*nomen nudum*); G. L. & N. Syn. Hep. 240. 1845 (as synonym).

Sendtnera Sauteriana Nees; G. L. & N. Syn. Hep. 240. 1845.

Schisma stramineum Dumort. Bull. Soc. Bot. Belgique 13: 123.

1874 (in part). Not 1831.

Herberta straminea Trevis. Mem. R. Ist. Lomb. III. 4: 396.

1877 (in part).

Brownish green, not glossy, growing in more or less extended mats: secondary stems erect or ascending, sparingly and irregularly branched, rigid, mostly 5–8 cm. long, about 0.35 mm. (or fifteen cells) wide and 0.3 mm. (or twelve cells) thick, the cells everywhere with strongly thickened walls: leaves imbricated, more or less secund, broadly ovate, mostly 1.2–1.6 mm. long and 0.75–1.1 mm. wide, bifid one half or a little more, the divisions (in explanate leaves), slightly or not at all curved, acute to acuminate, mostly 0.6–0.9 mm. long and 0.4–0.55 mm. wide, margin irregu-

* *Nyt Mag. f. Naturv.* 33: 223. 1893.

larly toothed near the base, the teeth mostly two to five on each side, sometimes small, sometimes larger and lobe-like; vitta indistinct even in the basal region, extending into the divisions but soon coming to an end, undivided portion about 0.25 mm. long and 0.35 mm. wide; cells of vitta mostly $40-70 \times 18 \mu$ in the basal portion and $30-40 \times 16 \mu$ in the divisions, marginal cells in the basal portion about 14μ in diameter, cells between margin and vitta about 16μ in diameter; thickenings distinct in the vertical walls, mostly $4-6 \mu$ wide; cuticle distinctly striolate-verruculose, especially near the base: underleaves similar to the leaves but shorter and more symmetrical: inflorescence unknown.

The following specimens have been examined:

AUSTRIA (TIROL): Kleiner Rettenstein near Jochberg, *A. Sauter* (distributed as *Sendtnera Sauteriana* in Rabenhorst's Hep. Europ. 33a); near Kitzbühel, August, 1882, *J. Braidler*; Rosskogel, *F. Arnold* (distributed as *Sendtnera Sauteriana* in Gottsche & Rabenhorst's Hep. Europ. 422); Sellraintal, August, 1912, *H. von Handel-Mazzetti* (distributed as *H. straminea* in Schiffner's Hep. Europ. Exsic. 468).

Müller and other writers cite the species from Bavaria and Salzburg, as well as from Tirol.

The present species bears a strong resemblance to the true *H. adunca* and it is not at all surprising that botanists have sometimes had difficulty in distinguishing them. Both normally grow in broad mats, their color is much the same except for the fact that *H. Sendtneri* seems never to be tinged with red or purple, their leaves are equally imbricated and divided to about the same extent, their divisions are less curved than in most species of the genus, and the vitta is poorly defined in both, the branches coming to an end far below the apices of the leaves. At the same time they exhibit excellent differential characters. The leaves in *H. Sendtneri* are relatively broader than in *H. adunca*, the same thing is true of the leaf-divisions, and the thickenings in the leaf cells are less conspicuous, those in the vertical walls being only about half as wide. The most striking differences between the two species, however, are to be found in the basal teeth. In *H. adunca*, as already noted, basal teeth are either absent altogether or else occur as a rare abnormality. In *H. Sendtneri* they form a conspicuous feature of the species. It is true that they

may not be present on every individual leaf. Nevertheless, if a series of leaves is examined, the majority will show the basal teeth clearly. Some of the teeth consist of single cells, but most of them are three to ten cells long and often two to four cells wide at the base. Occasionally an even larger, lobe-like tooth is present. Although the basal teeth are almost always marginal it is sometimes possible to demonstrate a surface tooth.

3. *Herberta Hutchinsiae* (Gottsche) sp. nov.

Jungermannia juniperina β Hook. Brit. Jung. pl. 4. 1812 (in part).

Sendtnera adunca β *Hutchinsiae* Gottsche; Rabenhorst, Hep. Eur. 210 (accompanying text). 1862.

Herberta adunca β *Hutchinsiae* Schiffn. Lotos 60: 54. 1912.

Yellowish or brownish green, sometimes tinged with red or purple, often somewhat glossy, growing in more or less extensive mats or in pendent tufts, sometimes mixed with other bryophytes: secondary stems erect, ascending or pendulous, rigid, mostly 5–10 cm. long but sometimes shorter, about 0.25 mm. (or fourteen cells) wide and 0.2 mm. (or twelve cells) thick, the cells everywhere with thickened walls, although showing a fairly marked difference between cortical and median regions: leaves imbricated, strongly secund, unsymmetrical, narrowly ovate, mostly 1.2–1.5 mm. long and 0.45–0.5 mm. wide, the divisions strongly curved and more or less divergent, acuminate to long-acuminate, mostly 0.8–1.2 mm. long and 0.2–0.25 mm. wide; margin normally entire; vitta distinct, extending far out into the divisions but hardly to the apices, undivided portion mostly 0.15–0.18 mm. long and 0.25–0.3 mm. wide; cells of vitta mostly $30\text{--}75 \times 14\text{--}18 \mu$ in the basal portion and $25\text{--}50 \times 18\text{--}20 \mu$ in the divisions, marginal cells in the basal region mostly $16\text{--}20 \mu$ in diameter, cells between margin and vitta mostly $18\text{--}24 \mu$ in diameter; thickenings distinct, in the vertical walls about 6μ wide; cuticle faintly but distinctly striolate-verruculose: underleaves similar to the leaves but symmetrical, squarrose, and with straight divisions: male inflorescences normally borne in an interrupted series in the upper part of a stem, more rarely on a lateral or ventral branch; bracts and bracteoles mostly in four to six series, similar to the leaves but with straighter and less divergent divisions and a broad basal pocket, about 1 mm. long and 0.45 mm. wide, margin subentire to sparingly and irregularly denticulate; antheridia mostly two or three in each axil: female inflorescence apparently always terminal on a stem, often with

one or more subfloral innovations; bracts and bracteoles similar, in about three series, those of the innermost series mostly 2.5–3.5 mm. long and 0.7–0.9 mm. wide, suberect and appressed to the perianth, bifid a little more than one half with slender, acuminate, subparallel divisions, margin copiously and shortly denticulate or dentate to or just above the level of the sinus, otherwise entire; bracts and bracteole of the other series a little shorter and often squarrose, the divisions usually more or less divergent, the margin varying from denticulate to coarsely and irregularly dentate; paraphyllia occasionally present, small and irregular; perianth ovate, not contracted at the mouth, about 3.5 mm. long and 0.8 mm. wide, divided for about half the length into six lanceolate, long-acuminate divisions, papillae numerous along the margins of the divisions near the base and on the inner surface of the perianth, usually sessile but sometimes borne on very short stalks: capsule brown, oval, about 1 mm. in diameter, splitting usually into six to eight valves; spores brown, about $25\ \mu$ in diameter, minutely echinulate; elaters brown, usually with two loose spirals, rarely with three, about $10\ \mu$ wide. [PLATE 8.]

The following specimens have been examined:

NORWAY: Lyse near Stavanger, July, 1897, *E. Jörgensen* (distributed as *H. adunca* β *Hutchinsiae* in Schiffner's Hep. Eur. Exsic. 466; specimens from the same locality listed by Kaalaas, as *H. adunca*, in *Nyt. Mag. f. Naturv.* 40: 247. 1902).

SCOTLAND: Moidart, Inverness, 1898, 1899 and 1901, *S. M. Macvicar* (listed as *H. adunca* in *Jour. Bot.* 37: [3]. 1899; specimens from same region distributed as *H. adunca* β *Hutchinsiae* in Schiffner's Hep. Europ. Exsic. 467); without definite locality or date, specimen from Hooker herbarium; Ben Vorlich, July, 1901, *S. M. Macvicar*; Ben Lavigh, July, 1901, *R. H. Meldrum*.

ENGLAND: Borrowdale, Cumberland, July, 1844, *Mr. Brown*; April, 1893, *W. H. Pearson*.

WALES: Craig-y-can, Merioneth, May, 1877, *C. J. Wild* & *W. H. Pearson* (distributed as *H. adunca* in Carrington & Pearson's Hep. Brit. Exsic. 42).

IRELAND: Bantry, *Miss Hutchins*; Killarney, *B. Carrington* (distributed as *Sendtnera adunca* β *Hutchinsiae* in Rabenhorst's Hep. Europ. 210); Brandon Mountain, *D. Moore* (distributed as "*Sendtnera juniperina* Nees = *Sendtnera adunca* Dickson" in Gottsche & Rabenhorst's Hep. Europ. 491); same locality, no date, *W. Mitten*, several specimens; same locality, 1881, *D. Mc-*

Ardle; Mangerton Mountain, no date, *W. Mitten*; Mt. Cromaglow, *R. Spruce*; without definite locality or date, specimen from the Hooker herbarium.

ALASKA: Sitka, collector and date unknown (specimen received from Lindberg, in the Austin herbarium); Yes Bay, August, 1895, *T. Howell 1810* (listed as *H. adunca* by the writer in Proc. Wash. Acad. Sci. 2: 309. 1900); Hot Spring, Baranof Island, June, 1899, *W. Trelease 1525a, 1808* (Harriman Expedition, listed as *H. adunca* by the writer, *l.c.*); Metlakatla, May, 1913, *R. B. Wylie 76, 97*; *T. C. Frye 109* in part; Ratz Harbor, June, 1913, *T. C. Frye 309*; Saltery Cove, June, 1913, *T. C. Frye 320*; Nichols Bay, June, 1913, *T. C. Frye 384*; Morse Cove, June, 1913, *T. C. Frye 446*; Brownson Bay, June, 1913, *T. C. Frye 470*; *A. S. Foster 517*; Augustine Bay, July, 1913, *T. C. Frye 561*; *A. S. Foster 677*; Port San Antonio, July, 1913, *T. C. Frye 605, 649*; Aats Bay, July, 1913, *T. C. Frye 925*. The specimens of Frye, Foster, and Wylie were collected under the auspices of the Kelp Investigation Expedition of the United States Bureau of Soils. They have already been listed by the writer, as *H. adunca*, in Bull. Torrey Club 41: 601. 1915.

BRITISH COLUMBIA: Fraser Reach, Princess Royal Island, June, 1899, *F. V. Coville & T. H. Kearney* (Harriman Expedition, probably the basis for Osgood's record of *H. adunca* in U. S. Dept. Agric. Biol. Surv. Bull. 21: 14. 1901); Port Renfrew, August, 1902, *S. A. Skinner* (listed as *H. adunca* by the writer in Postelsia 1906: 228); Ucluelet, 1909, *J. Macoun 2* (specimens from same locality distributed as *H. adunca* by Miss Haynes in Amer. Hepat. 72 and by Macoun in Can. Liverworts 83); Swanson Bay, May, 1913, *T. C. Frye 1174* (Kelp Expedition).

The specimens collected by Miss Hutchins at Bantry, Ireland, and now preserved in the Mitten herbarium at the New York Botanical Garden, should be considered the type of the species.

The following records for *H. adunca* from Alaska should also be noted: without definite locality, date or collector's name (listed by Underwood in Zoe 1: 366. 1891); St. Paul Island, Pribolof Islands, *C. H. Merriam* (listed by Merriam in Proc. Biol. Soc. Washington 7: 150. 1892). Underwood's record was probably based on Lindberg's specimens cited above. Merriam's record,

however, was based on specimens in the United States National Herbarium, which, in the writer's opinion, represent a slender form of *Anthelia julacea* (L.) Dumort. This species is now known from several localities in Alaska, and additional specimens, essentially like those of Merriam, were collected on St. Paul Island, in 1897, by T. C. Kincaid (49).

The narrower and more deeply divided leaves of *H. Hutchinsiae*, with their more slender and strongly curved divisions will usually distinguish the species from *H. adunca* at a glance. In doubtful cases the distinct vitta extending far out into the divisions will decide the determination. The more gradual tapering of the divisions is clearly brought out by counting their width in cells. In *H. Hutchinsiae*, if the counts are made at a distance of 0.2 mm. from the apices, the divisions are found to have a width of from two to four cells; in *H. adunca* the corresponding counts will usually give from five to eight cells. Counts at the bases of the divisions are much less conclusive, on account of the fact that the divisions in *H. Hutchinsiae* are relatively longer, the bases thereby being often as wide as in *H. adunca*.

Among the specimens listed above, those from Norway are somewhat aberrant. Although some of the shoots conform closely to the type, others bear leaves which are considerably larger. One of the largest leaves measured had a length of 2.4 mm. and a width of 0.95 mm.; another, a length of 2 mm. and a width of 1 mm. The dorsal divisions of these measured, respectively, 1.2×0.45 mm. and 1.05×0.4 mm. Since these leaves are relatively broader than is usual, it might appear at first sight as if the large-leaved shoots approached *H. adunca*, but the distinct vittae present would seem to preclude this idea. In all probability they represent shoots developed under unusual conditions, perhaps exceptionally favorable from a nutritive standpoint; the large leaves might then be regarded as abnormal.

The androecia in *H. Hutchinsiae* are not absolutely constant in position. In normal cases they are borne on the secondary stems just as in *H. adunca*. Under these circumstances an androecium usually proliferates at the apex and then produces a new androecium after a short series of vegetative leaves. In several instances, however, androecia on ventral or lateral branches have been

observed. These are apparently never produced unless the growth of the main male axis is brought to an end in some way, possibly through the failure of an androecium to proliferate, possibly through an accident of some sort. In either case a branch tends to take the place of the main axis and to assume its functions, precisely as a ventral branch of a sterile axis or a subfloral innovation would do. When, therefore, an androecium is borne on a branch of this character, its position can not be regarded as typical.

These considerations gain in significance when *H. Hutchinsiae* is compared with *H. dicrana* (Tayl.) Trevis., a closely related species of the Himalayas. The writer's knowledge of this species is largely based on specimens received from Levier and collected by Decoly and Schaul (782) near Kurseong in Sikkim-Himalaya, in May, 1899. These specimens contain both male and female plants and are of especial interest because they served as the basis for Schiffner's statements regarding the androecia of *H. dicrana*.* He notes their occurrence on the ends of branches, their small size, the small number of bracts (about four pairs) which they bear, and the fact that they are sterile at the apices. The branches which bear the androecia are ventral and vary greatly in length. Sometimes the development of the antheridia brings the growth of the branch to an end, but a sterile proliferation of the androecium often occurs. The formation of the male branches seems to be a perfectly normal process and is not preceded by a cessation of growth of the main stem as in *H. Hutchinsiae*. It follows, therefore, that what occurs abnormally in the northern species has become normal in the Himalayan species. It should be noted, however, that ventral androecia are not absolutely constant even in *H. dicrana*. One example was observed where the androecium was borne on a main stem; it had somewhat larger bracts and bracteoles than the ventral androecia but resembled them in other respects. Aside from the difference in the position of the androecia, *H. dicrana* resembles *H. Hutchinsiae* very closely. The leaves and underleaves, the bracts and bracteoles, and the perianths are much the same in the two species, although the divisions of the leaves in *H. dicrana* usually are less strongly curved. The latter species, moreover, is slightly larger, the leaves are less crowded and the thickening of the cell-walls is less pronounced.

* Hedwigia 50: 148. 1910.

4. *Herberta tenuis* sp. nov.

Schisma juniperinum Sulliv. Musc. Alleg. 258. 1846. Not Dumort.

Sendtnera juniperina Sulliv.; A. Gray, Man. 689. 1848. Not Nees.

Herberta adunca Underw. Bot. Gaz. 14: 195. 1889. Not S. F. Gray.

Yellowish or brownish green, rarely tinged with red, growing in more or less extensive mats: secondary stems erect or ascending, sparingly and irregularly branched, rigid, mostly 2–4 cm. long, about 0.15 mm. (or ten cells) wide and 0.13 mm. (or nine cells) thick, outer layer of cells with strongly thickened walls, interior cells with slightly thickened walls: leaves scattered to loosely imbricated, subsquarrose to slightly secund, a little unsymmetrical, subovate, mostly 0.9–1 mm. long and 0.3–0.35 mm. wide, bifid two thirds to three fourths, divisions (in explanate leaves), divergent, slightly or not at all curved, long-acuminate, mostly 0.6–0.7 mm. long and 0.15–0.18 mm. wide, margin entire or with an occasional basal tooth; vitta distinct, extending far out into the divisions but not to the apices, undivided portion about 0.1 mm. long and 1.5 mm. wide; cells of vitta mostly $20\text{--}55 \times 14 \mu$ in the basal portion and $20\text{--}35 \times 14 \mu$ in the divisions, marginal cells in the basal region about 14μ in diameter, in the divisions about 17μ , cells between margin and vitta about 20μ ; thickenings distinct but not so strongly developed as in most species, in the vertical walls mostly $3\text{--}4 \mu$ wide; cuticle minutely striolate-verruculose: underleaves similar to the leaves but symmetrical; inflorescence unknown. [TEXT FIGS. 21–29.]

The following specimens have been examined:

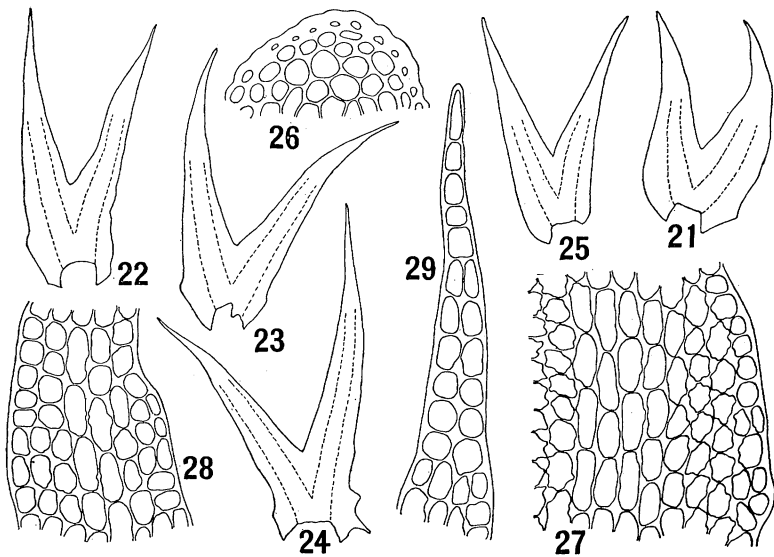
NEW YORK: Kaaterskill Falls, Catskill Mountains, *C. H. Peck* (listed by Peck, as *Sendtnera juniperina*, in Rep. New York State Mus. Nat. Hist. 19: 70. 1866; both “Cauterskill” Falls and High Peak, Catskill Mountains, are mentioned here); Austin’s Hep. Bor.-Amer. 82, distributed as *Sendtnera juniperina*, is also *H. tenuis* and may possibly include some of Peck’s material, the label reading: “Catskill Mountains, New York, *Peck*, Greenwood Mts., N. J., *Aust.*; also in the Alleghanies southward.”

NEW JERSEY: Greenwood Mountains, Passaic County, November, 1866, *C. F. Austin* (listed by Britton, as *H. adunca*, in Cat. Pl. New Jersey 351. 1889); Austin’s Hep. Bor.-Amer. 82 (see above) is probably made up largely of material from this locality.

PENNSYLVANIA: Stony Creek, Somerset County, *F. Wolle*.

VIRGINIA: summit of White Top Mountain, Washington County, May, 1892, *A. M. Vail & E. G. Britton* 9, 91, and numerous unnumbered specimens; same locality and date, *J. K. Small* 77, 79 (listed by Small & Vail, as *H. adunca*, in Mem. Torrey Club 4: 193. 1894).

WEST VIRGINIA: Tibbs Run, Monongalia County, September, 1892, *C. F. Millspaugh* 1659 (listed by Millspaugh, as *H. adunca*, in Prelim. Cat. Fl. W. Va. 496. 1892); Quarry Run, Monongalia County, 1903, *A. LeR. Andrews*.



FIGS. 21-29. *HERBERTA TENUIS* EVANS

21-25. Leaves, $\times 40$. 26. Transverse section of a mature stem, $\times 225$. 27. Cells from the lower part of a leaf, including the vitta just above the forking. $\times 225$. 28. Cells from the upper part of a dorsal leaf-division, $\times 225$. 29. Cells from the apex of a division, $\times 225$. FIG. 21 was drawn from specimens distributed in Austin's Hep. Bor.-Amer. 82; the remaining figures, from the type specimen.

NORTH CAROLINA: "in montibus Carolinae," *F. Michaux* (listed by Michaux, as *Jungermannia sertularoides*, in Fl. Bor. Amer. 2: 278. 1803), the label reading as follows: "Junga sertularoides Rich. Fl. b. Am. a Jung. trichophylla vox aut non distincta! Hb. Hooker"; "in montosis editissimis Carolinarum,"

1843, *A. Gray & W. S. Sullivan* (distributed, as *Schisma juniperinum*, in Sullivan's *Musc. Alleg.* 258, and listed by Sullivan, as *Sendtnera juniperina*, in *A. Gray, Man.* 689. 1848); top of Black Mountain, June, 1850, *L. Lesquereux*; Grandfather Mountain, August, 1891, *J. K. Small* 32 (also distributed, as *H. adunca*, in Underwood & Cook's *Hep. Amer.* 126); Grandfather Mountain, September, 1901, *G. F. Atkinson* 11420, 11501 (listed by Andrews, as *H. adunca*, in *Bryologist* 17: 59. 1914); near Shulls Mills, Blue Ridge Mountains, September, 1901, *G. F. Atkinson* 12054 (listed by Andrews, *l.c.*).

Dr. Small's specimen from North Carolina, No. 32, may be designated the type.

Two additional records for *H. adunca* from the eastern United States may likewise be noted, namely: Carbon County, Pennsylvania, *E. A. Rau* (listed by Porter in *Cat. Bryoph. & Pteridoph. Pennsylvania* 9. 1904), and mountains of western North Carolina, 1907, *A. J. Grout* (listed by Grout in *Bryologist* 12: 54. 1909). In all probability these records were based on *H. tenuis*.

The present species is closely related to *H. Hutchinsiae* but is considerably smaller. Although at first sight the small size might appear to be due to poor development, the study of a large series of specimens from many localities shows pretty conclusively that this is not the case. The size is of course subject to more or less variation, as in all species of *Herberta*, but the measurements of the leaves given in the description represent a fair average of the more robust plants studied, and are only about two thirds as great as the corresponding measurements in *H. Hutchinsiae*. The difference in size is brought out with especial clearness by counting the width of the basal portion in cells between the vitta and the margin. In *H. Hutchinsiae* such a count would give from five to seven cells; in *H. tenuis* from three to five cells. Aside from the difference in size the slightly curved or straight divisions in *H. tenuis* and the thinner cell-walls will distinguish the species from *H. Hutchinsiae*, where the divisions are normally strongly curved and the thickening of the cell-walls much more distinctly marked.

The basal teeth in *H. tenuis*, although an inconstant feature, deserve a few words of comment. When they occur there may be one or, rarely, two teeth on each side, and the underleaves tend

to produce them more frequently than the side-leaves. The teeth are of fair size, often involving several cells, and may be rounded or sharp. In the latter case they are especially conspicuous (TEXT FIG. 24). It has already been noted that teeth form an important feature of the leaves in *H. Sendtneri*, whereas in *H. adunca* and *H. Hutchinsiae* the margin is normally entire. *H. tenuis* occupies an intermediate position in this respect, the teeth being less frequent than in *H. Sendtneri* but more frequent than in either of the other species.

The present paper is based largely on material in the herbarium of Yale University. This has been supplemented by specimens from the Taylor herbarium at Harvard University and from the herbarium of the New York Botanical Garden. Additional specimens have been received from Prof. A. LeRoy Andrews of Cornell University, from Mr. S. M. Macvicar of Invermoudart, Scotland, and from Mr. C. Jensen of Hvalsö, Denmark. The writer would express his sincere thanks to all who have aided him in his work.

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YALE UNIVERSITY.

Explanation of plate 8

HERBERTA HUTCHINSAE (Gottsche) Evans

FIGS. 1-3. Leaves, $\times 40$.

FIG. 4. Cells from the lower part of a leaf, showing the basal vitta, $\times 225$.

FIG. 5. Cells from the dorsal base of a leaf, showing two rudimentary teeth, $\times 225$.

FIG. 6. Cells from the upper part of a dorsal leaf-division, $\times 225$.

FIG. 7. Cells from the apex of the same division, $\times 225$.

FIGS. 8, 9. Perigonal bracts, $\times 40$.

FIG. 10. Perichaetial bract from next to the last pair, $\times 27$.

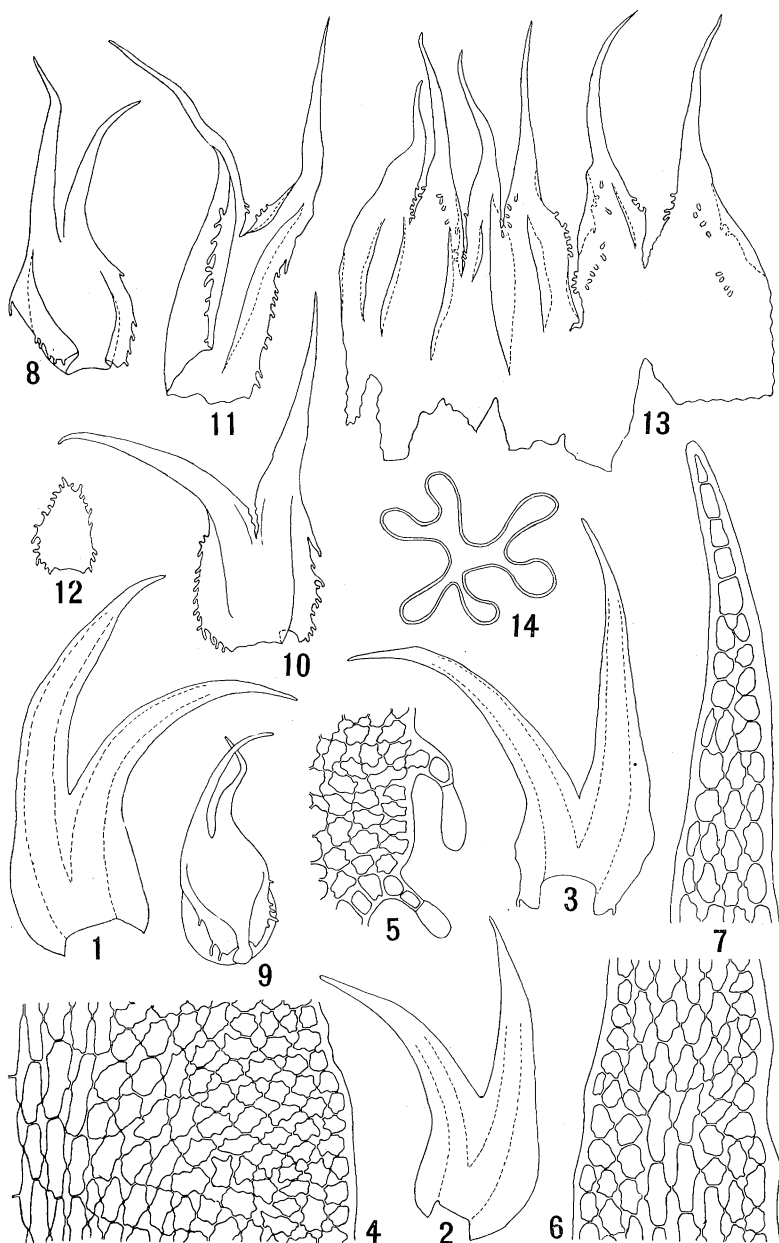
FIG. 11. Perichaetial bract from the innermost pair of the same involucre, $\times 27$.

FIG. 12. Paraphyllum from the same involucre, $\times 27$.

FIG. 13. Perianth, spread out flat, $\times 27$.

FIG. 14. Transverse section of perianth, $\times 40$.

FIG. 1 was drawn from Irish specimens collected by B. Carrington and distributed in Rabenhorst's *Hep. Europ.* 210; FIG. 2, from Scottish specimens collected by S. M. Macvicar and distributed in Schiffner's *Hep. Europ. Exsic.* 467; the remaining figures, from specimens collected by T. C. Frye at Port Antonio, Alaska, 649.



HERBERTA HUTCHINSIAE (GOTTSCHE) EVANS